THE HIND FOOT OF *YOUNGINA* AND FIFTH METATARSAL IN REPTILIA

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In a paper on the Classification of the Reptilia (Goodrich, 1916) it was maintained that this Class is not a simple monophyletic group, but is composed of three main divisions: first a basal group of relatively primitive forms, the Protosauria, derived from some amphibian-like ancestor and retaining the complete bony roof of the temporal region of the skull; and two diverging branches, the Theropsida and the Sauropsida (Huxley's original term used in a restricted sense). The branch Theropsida (including the orders Mesosauria, Ichthyosauria, Plesiosauria = Sauropterygia, Pelycosauria, Dinocephalia, Dicynodontia, Theriodontia, and related forms) leads towards the Class Mammalia, and has only one temporal fossa pierced in the roof of the skull. Following Osborn (1903) these reptiles are often called the Synapsida. The branch Sauropsida (including the orders Eosuchia, Protorosauria, Rhynchocephalia, Squamata [placed here on the assumption that they have lost one or both of the temporal arches], Pseudosuchia, Phytosauria, Crocodilia, Pterosauria, Saurischia, Ornithischia) leads towards the Class Aves. In the Sauropsida two temporal fossae are developed, and they are often called the Diapsida (Osborn, 1903). The general conclusion that the Reptilia have diverged into these two main branches with synapsidan and diapsidan skulls had already been accepted by many authorities, and the chief object of my paper was to show that this conclusion was further strongly supported by evidence derived from the structure of the heart and of the skeleton of the hind-foot.

Of the sauropsidan specialization of the heart and bases of the aortic arches (further dealt with in greater detail in my later book: Goodrich, 1930) little need be said here, except that the mammalian heart and arches must have been evolved along very different lines from a more amphibian-like general structure. It is an important fact that the sauropsidan type of heart is fully developed in all living Reptilia, including the Chelonia.[1]

The other evidence comes from the tarsus and metatarsus, and concerns chiefly the peculiar modification of the fifth metatarsal which, in Sauropsida, tends to be shortened while its proximal widened end becomes strangely bent and 'hook-shaped' or 'hooked', as it may be called for short. It thus acquires

[1] So far as I am aware no palaeontologist has taken into account the vascular system when classifying the Reptilia, nor appreciated its great significance. Probably similar divergences could be found in other organs, such as the brain.

a very characteristic shape due to the development of a strong process extending medially (forwards) to articulate closely with the enlarged fourth distal tarsal at a level proximal to that of the other metatarsals, and an outstanding process at its outer angle (Fig. 1).

This modification of the fifth metatarsal is accompanied by the reduction of the fifth distal tarsal, and also is possibly related to the development of the mesotarsal articulation so characteristic of all the Sauropsidan reptiles and their offspring the birds. That the hook-shape of the fifth metatarsal was originally of functional significance seems highly probable, though no one as yet appears to have explained exactly what this function may have been. The detailed descriptions given by Perrin (1895) and Osawa (1898) of the musculature of the foot of *Sphenodon* throw little light on the problem.

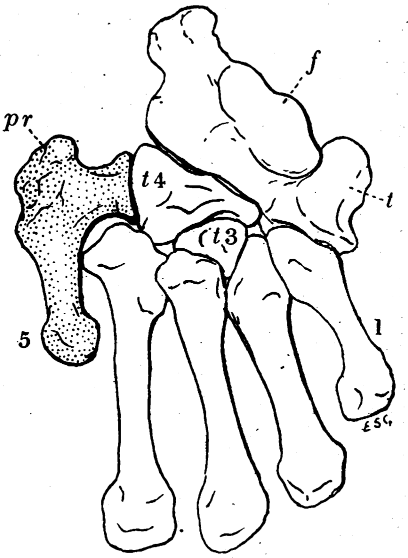


Fig. 1. Tarsus and metatarsus of *Varanus salvator*, Saur. Right foot, dorsal view. Fifth metatarsal shaded. *f*, articular facet for fibula on proximal fused tarsals; *pr*, outer process; *t*, articular facet for tibia; *t3*, third distal tarsal; *t4*, fourth distal tarsal.

It has been pointed out (Goodrich, 1916, p. 264) that 'the hook-shaped metatarsal does not seem to be closely related to any particular mode of life or method of progression, being essentially the same in reptiles of the most diverse habits'. It is seen in all groups of living reptiles with free outstanding limbs, is obvious in Lacertilia (Fig. 1), Chelonia, and *Sphenodon*, and can be traced in Crocodilia in spite of the great reduction of the fifth toe. Moreover, once acquired the modification seems never to be entirely lost, even when the foot becomes transformed into a paddle adapted for swimming—for instance in *Desmachelys* (Völker, 1913), and Mesosauria (Osborn, 1899). Further, the hook-shaped metatarsus was already developed not only in Triassic (*Howesia*, *Aëtosaurus*, etc.), but even in Permian times (*Palaeagama*, *Protorosaurus*).[1]

Lastly, a careful search of the literature and examination of all available specimens seems to warrant the following general statements: that the modified fifth metatarsal never occurs outside the Branch Sauropsida; that no

[1] The following list includes interesting genera of early fossil reptiles known to have a hooked fifth metatarsal: Eosuchia: *Palaeagama* (Broom, 1926); *Howesia* (Broom, 1906); *Noteosuchus* = *Eosuchus* (Broom, 1925). Protorosauria: *Protorosaurus* (v. Meyer, 1856; Seeley, 1887); *Sauranodon* (Lortet, 1892). Pseudosuchia: *Euparkeria* (Broom, 1913); *Aëtosaurus* (v. Huene, 1920). Rhynchosauria: *Rhynchosaurus* (Huxley, 1887; A. S. Woodward, 1906). Rhynchocephalia: *Homoeosaurus* (Lortet, 1892); *Champsosaurus* (Brown, 1913). Phytosauria: *Rhytidodon* (McGregor, 1909).

reptile living or extinct, and known for certain to possess a diapsid skull, has been found without it.[1] These facts are surely of significance.

Therefore, when Broom (1921) described the Upper Permian South African reptile, *Youngina capensis*, as having a diapsid skull but an unmodified fifth metatarsal, I was greatly surprised and interested. Here at last there seemed to be an exception to the rule. Of course it is to be expected that intermediate early forms may be found showing incipient stages in the modification. There is no reason to believe that the diapsid structure of the skull is directly related to the hook-shape of the fifth metatarsal. Doubtless these two specializations evolved independently, and possibly one considerably before the other.

The excellent descriptions given by Broom (1922, 1924) of the skull of *Youngina* prove without doubt that it was not only provided with two temporal fossae, but also that it closely resembled the skull of *Sphenodon*, a genus to which he considers *Youngina* to be related. Broom's careful work on the skeleton of the hind foot of *Youngina* is almost entirely founded on a single left foot, somewhat crushed but sufficiently complete to provide material for a good reconstruction (Broom, 1921, Fig. 20). The tarsus is remarkable for the retention of a small fifth distal element attached to the usual enlarged fourth. The fifth metatarsal Broom says, 'is a long slender bone, nearly as long as the fourth metatarsal, and it shows no trace of the peculiar hooking. The upper end is expanded, and the outer process probably was attached to the fibulare by a ligament' (p. 152).

I am very grateful to Dr Broom for having sent me this precious specimen to examine. After careful scrutiny I am unable to agree with some of his con-

[1] Considering how striking is this character it is astonishing how little importance has been attributed to it by those authors who have attempted to classify the Reptilia. Williston mentions (1925) but does not insist on it. Watson (1917), although admitting that it is present in chelonians, rhynchocephalians, thecodonts, crocodiles, dinosaurs, and squamata, refrains from attributing much weight to it 'because it is difficult to believe that all these forms can have been derived from some advanced Cotylosaurian ancestor'. He suggests that it is perhaps an arboreal adaptation, which may have originated separately. But surely it is still more difficult to believe that this special form of fifth metatarsal has arisen independently so many times, and especially that the Chelonia should have had arboreal ancestors. Moreover, the Chameleons, probably the most specialized of all reptiles for arboreal life, are just those lizards in which the modification is least obvious!

Piveteau (1926), in his interesting description of the Permian reptiles of Madagascar, states that the fifth metatarsus of *Tangasaurus* is shortened and (at stage A) 'présente une forte dilatation de la tête proximale', but that at later stages 'sa tête supérieure n'est pas recourbée' although widened. Nor could I discern that it is distinctly hook-shaped in a large specimen Mr Parrington kindly allowed me to examine at Cambridge. The affinities of *Tangasaurus* are still uncertain since the structure of its skull is not fully known, and the evidence from the hind foot seems to be indefinite. Possibly we have here an early form in which the modification of the metatarsal is only beginning. Piveteau (1926) goes on to say that the modification of the fifth metatarsal cannot be considered as 'fondamental dans la classification des Reptiles. Son apparition sporadique dans les groupes les plus divers montre qu'on ne peut lui attribuer une pareille importance'. But, as a matter of fact, as indicated above, its distribution far from being sporadic is remarkably constant. It occurs in some degree not only in all Chelonia, but also in all 'Diapsida', and in these only so far as we know.

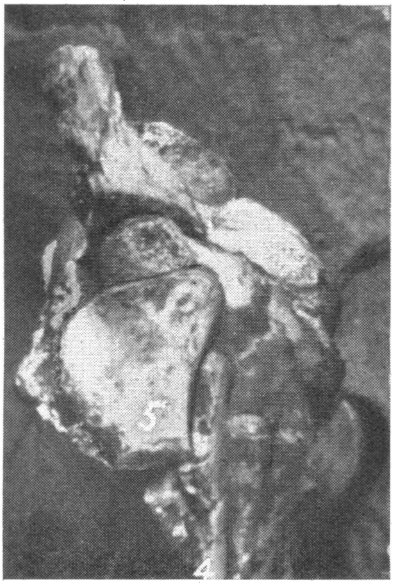
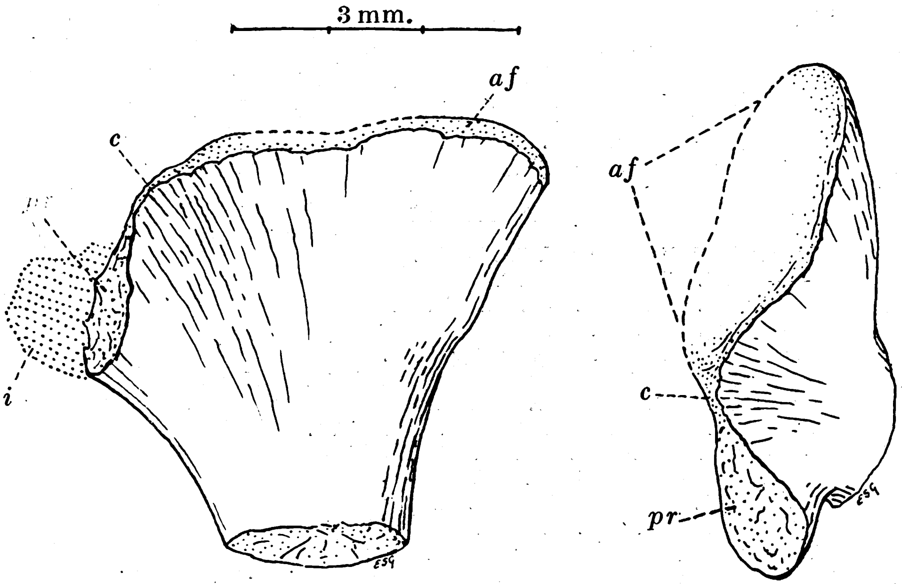


Fig. 2. Photographs of part of skeleton of left hindfoot of *Youngina capensis*, Broom, showing ventral surface of fifth metatarsal displaced, 5; it is outlined in black. 4, fourth metatarsal cut short distally. Enlarged.



Figs. 3, 4. Drawings of ventral and proximal views of fifth metatarsal of *Youngina*; showing, *af*, articular facet for fourth and fifth distal tarsals, *c*, constriction between it and, *pr*, broken outer process, *i*, impress of process on matrix. Concealed outline drawn in broken line.

clusions stated above. Fig. 2 is a photograph showing the fifth metatarsal as it lies somewhat displaced, and Fig. 3 is a drawing of the same bone. Its main shaft is broken short, and its original length can only be conjectured from an impress on the matrix. The fifth appears to have been considerably shorter than the fourth metatarsal. It is true that the expanded proximal end is not markedly hook-shaped, yet certain of its features seem clearly to indicate that it is to some extent modified in that direction. The proximal edge of the expanded head is subdivided by a constriction into an inner rounded elongated articular surface (Fig. 4), and an outer projecting process now partly broken away. The persistence of an impression on the matrix (Figs. 3, 4) shows that this process must have been of considerable size. While the articular facet seems to have been, as usual in the 'modified' type, closely connected with the large fourth distal tarsal (and also probably with the reduced fifth distal tarsal), the outer projection must surely represent the similar process so characteristic of a typical hook-shaped metatarsal. Such an outstanding process is not found on normal fifth metatarsals. The conclusion seems inevitable that the fifth metatarsal of this Upper Permian Eosuchian *Youngina* was, at all events to some extent, modified towards the hook-shaped type.

SUMMARY

After discussing the importance of the modification of the fifth metatarsal as a constant feature in that branch of the Reptilia to which the name Sauropsida may be applied (and in which the diapsidan skull occurs) this metatarsal is described in *Youngina*, an Upper Permian Eosuchian from South Africa, hitherto considered to be of the unmodified type. It is maintained that the fifth metatarsal of *Youngina* shows distinct signs of modification towards the sauropsidan hook-shaped type.

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